

knobs. The specimens illustrated have very little in common with those shown by Bresadola.

Singer (1949) accepts *A. strobiliformis* but omits *A. solitaria* from his list.

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(To be continued)

SEX RATIO AND VARIATION IN *APUS AUSTRALIENSIS* SPENCER AND HALL

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I. SEX RATIO

In the absence of comprehensive works on Australian natural history local field workers are forced to use overseas texts. Commonly used text-books all mention that the males of *Apus* are rare. Examples of such statements are as follows:—

"Males are rare, reproduction being normally by parthenogenesis" (Borradaile *et al.*, p. 362). "The large majority of individuals of *Lepidurus* and *Apus* are females, males are of comparatively rare occurrence" (Parker & Haswell, vol. 1., p. 395). "One species has been shown to be hermaphrodite; in others males are occasionally found, but reproduction appears to be, as a rule, parthenogenetic" (*ibid.*, p. 396).

The statements appear to relate to *Apus caneriformis* the common *Apus* of England and Europe but while these

texts are locally used as standard references the statements above are generally construed to indicate that the local species of *Apus* probably follow the European pattern.

Well-known Australian faunal works tend to support this view. Thus Spenceer (1896, p. 228) writing of *Apus australiensis* says: "It is worth noting that every species yielded specimens of both males and females. In the Estheriadae the numbers may, roughly speaking, be said to be about equal and amongst 58 specimens of *Apus*, 6 are males."

He adds (p. 234): "It will be noticed that male specimens are not relatively infrequent, though their number is considerably less than that of the females." On this same page it is mentioned that serial sections of gonads revealed no trace of sperm in the ovaries thereby eliminating the possible existence of hermaphroditism in these specimens.

On a visit to Morawa during the period May 6-13, 1953 *Apus* were found to be abundant in the salt lakes system then flowing strongly as a result of rains brought by a cyclone of northern origin late in March. These rains had been supplemented by further falls in April. The resulting floods filled salt lakes from Austin in the north to Yarra Yarra at Three Springs. The waters had receded from their highest level but were still flowing strongly.

In the shallow water *Apus* were common and judged by the number of copulating pairs males appeared to be frequent. A sample taken by hand at one situation yielded the following:—

By container.				Total no. of animals	Limits of deviation, for small samples, which agree with equal- ity (from Simpson and Roe, Table 9).		
♀	%	♂	%		Size of sample		
1. 81	65.3	43	34.7	124	—	—	—
2. 12	70.5	5	29.7	17	15	14	: 1
3. 12	60.0	8	40.0	20	20	17	: 3
4. 17	68.0	8	32.0	25	25	20	: 5
122	65.6	64	31.4	186			

Deviation from 50%, 29 or 15.6%.

Spenceer (p. 228) has females, 52, 89.6%; males, 6, 10.4%.

The samples above were not truly random. Consequently there may be bias in the figures, but even so males seem to be too abundant to be called rare. Certainly the Morawa figures do not agree with Spenceer's but what do these figures really mean in relation to the presence and abundance of males in the Australian species? Further, in this connection, the Kurrawang figures (see below) show rough agreement with those from Morawa.

Apus has one generation per season and in any sexually reproducing animal where sex is controlled genetically it is a reasonable assumption that male and female gametes should be equal, namely 50% males and 50% females. If we make the assumption that at the time of sampling the sexes should also be equal we

can proceed to a test to determine whether the figures previously given support this assumption, in a statistical sense, by the formula for Standard Error (see Weatherburn, 1949) which gives:

$$\begin{aligned} \text{SE} &= 6.8 \text{ or } 3.68\% \\ \text{Deviation} &= 29 \text{ or } 15.6\% \end{aligned}$$

i.e. the *deviation* is more than four times the standard error. Inspection of Tables show that the chance of an error of this magnitude being due to errors of sampling is 16,000:1. Clearly this indicates that the figures do not agree with the assumption that males and females should be equal.

Inspection of Table 9 (in Simpson and Roe, 1939, as shown by Mayr, 1953, p. 129) tells us that in a single sample, samples nos. 2-4 are within the limits of error for the numbers used and therefore individually do not invalidate the assumption in regard to sex frequency. However, the samples no. 2-4 all deviate in the same direction and since they are consistent the deviation cannot be due to errors of sampling, i.e. the deviation is real.

To what may we ascribe the deviation? One possibility is that there is a differential death rate between the sexes, i.e. males may not be as hardy or survive as long as females. In this connection it should be remembered that the waters had been present since March 20-21, i.e. the *Apus* were almost 7 weeks old. (We have the observation of Spence (1896), supported by other field observers, that these crustaceans are sexually mature within 2 weeks of hatching.) A different mortality in the sexes, therefore, cannot be ruled out as one cause of the observed discrepancy in the sex ratio; a higher mortality among males is a common and widespread phenomenon in many animals.

A second possibility is associated with the existence of parthenogenesis. The statement from Borradaile *et al.*, already quoted, may only apply to *A. cancriformis* at the latitude of Europe and that from Parker and Haswell may be a generalisation based on familiarity of the life history of too few species. Hesse *et al* (1949, p. 361) state: "Parthenogenetic development in Entomostraea is more and more limited towards the equator, though scarcity of males in tropical Cladocera is reported. This is not true of the phyllopods and the ostracods. Although there are species of euphyllopods in the colder regions among which males have never been found or are very rare, males are in the majority in the collections thus far made of African species (*Limnadia*, *Lepidurus*, *Apus*, etc.)."

This passage would indicate that the extracts quoted from Borradaile and Parker and Haswell need not apply to the Australian species of *Apus*.

White (1945, p. 285) gives details of the parthenogenetic polyploid races of *Artemia* and (p. 286) discusses the polyploid races of the isopod *Trichoniscus* in which the parthenogenesis is associated with resistance to drought (Southern France), or extreme cold (Scandinavia, Iceland, where the bisexual races are absent). In the polyploid races males are few (1-2% of the population).

Parthenogenetic races of *Cypris fuscata* (Ostracoda) appear to be triploid. Those of *Daphnia pulex* (Cladocera) may be hexaploid (*op. cit.*, p. 287).

White, writing on the sex determination of the occasional males of the polyploid races of *Artemia*, says: "No doubt the bisexual race represents the original condition; unfortunately, nothing is known about its method of sex determination, so that it is scarcely worth while speculating as to the way in which occasional males are produced in parthenogenetic races."

Makino (1951, pp. 47-59) indicates that the above is essentially the state of knowledge at present. Polyploidy is apparently especially important in producing cold-hardiness in plants, e.g. all the grasses of Spitzbergen are polyploids (George, 1953).

Parthenogenesis is the only manner in which polyploids can reproduce, for assuming that one female increased the chromosome complement then sperm from normal (diploid) males will be inviable with the polyploid, reproduction without the male is the only way in which the strain can propagate. Because the specimens obtained at Morawa were not suitably prepared no chromosome count has been made but the presence of a reasonable frequency of males in the population indicates that polyploids are not abundant or dominant in the population.

II. VARIATION

Spencer (1896, p. 231), in the definition of *Apus australiensis*, states the number of apodous abdominal segments to be "about twelve" and records the species from Coolgardie and Hannans as well as from Central and South Australia and places east of this. Henry (1924, p. 124) discusses the variability in *Apus australiensis* but makes no mention of apodous segments. Wolf (1911, pp. 260-263) restricts the definition of *A. australiensis* to females and males having twelve apodous segments, he then erects two additional species as follows:—

Species	Locality	Apodous segments
<i>A. gracilis</i>	Hannan's Lake Kal-goorlie	female, 8 or 9; male, 12.
<i>A. strenuus</i>	Finke River, Hermannsburg	female, 10 or 11; male unknown

In view of the fact that meristic characters are usually variable it is of interest to list the variability of the Morawa specimens, a random sample from these gave:—

Locality	Sex	Number of apodous segments						Total no. of animals
		7	8	9	10	11	12	
Morawa ..	females ..	26	33	3	—	—	—	62
	males ..	—	6	11	3	—	—	20
Kurrawang ..	females ..	12	15	2	9	13	6	57
	males ..	—	1	7	10	2	6	26

The Kurrawang figures are a random sample taken from a collection made by Dr. D. L. Serventy in March, 1937.

From these figures it is apparent that the Morawa population is relatively homogenous and about the figures for *A. gracilis* females. However, the figures for males do not agree.

The figures from Kurrawang are more informative. Here the female range is complete and the males show a range from the lowest Morawa figure to that typical for *A. australiensis*. It should be pointed out that this sample included a great variation in absolute size of the animals. However females carrying eggs indicated that there is no correlation observable between size and number of apodous segments.

Mayr *et al* (1953) regard meristic (i.e. countable) characters as good taxonomically because (a), they are discrete, and (b), are less liable to error than measurements or ratios. However, before these characters can be used in a definition it is important to have an idea of the range and cause of variation in the population. Taning (1952), in a review, has assembled evidence that the number of vertebrae in certain fish species vary according to the temperature conditions to which the embryos are subjected; also other factors such as oxygen content and salinity of the water may affect such meristic characters. From this it is clear that experimental work is necessary to determine the genotypic control of such characters.

In the case of *Apus* it is interesting to refer to Alexander's report on a collection he made at two localities in the Kalgoorlie area:

Site	Source of water	Composition	Species present
Lakeside	Fed from Mundaring pipeline	Chlorine 0.01% Solids 0.05%	<i>A. australiensis</i>
Hannan's Lake	Depression in lake	Chlorine 0.69% Solids 1.40%	<i>A. gracilis</i>

These data, read in conjunction with the review of Taning, would indicate that chlorine, at least, may be one of the causes of variability in the genus *Apus*. The small size of Wolf's samples cannot give a reasonable picture of population variability and, taking into account the variation recorded above, it is clear that the evidence available at present does not support the existence of more than one species of *Apus* in Australia. The evidence indicates that 7 to 12 apodous segments fall within the range of *A. australiensis* and that the forms described under the names of *A. gracilis* and *A. strenuus* are only phenotypic variants. The names must be considered as pure synonyms of *australiensis*.

The eggs of *Apus* are presumably wind distributed during drought and there is, therefore, likely to be a good deal of admixture between western and eastern Australia. Under such conditions it seems unlikely that the geographic isolation necessary for speciation would be present. Thus *Apus* would agree with *Lepidurus*, which has one species, *viridis*, throughout Australia, and with *Artemia salina*, where the one species is world-wide.

Observations in the field on the variability in the number of apodous segments in *Apus*, in conjunction with environments and seasonal conditions are highly desirable.

SUMMARY

1. Males are considerably more common in *Apus* than has been reported in the literature quoted.
2. The samples discussed do not indicate that males and females are equally abundant.
3. The discrepancy observed in the samples when measured against the expectancy of equality cannot be due to error in sampling.
4. The marked difference in frequency of males and females may be due to difference in mortality in the two sexes. This cannot be checked because samples of the crustaceans over the history of this flooding were not taken.
5. Reference to literature would indicate that parthenogenesis and absence of males is characteristic of phyllopods in high latitudes with lower temperatures.
6. Further work needs to be done, by conveniently situated naturalists, on the biology of *Apus* so that the life history and other details of this characteristic local form are better known.
7. It is suggested that there is only one species of *Apus* in Australia, namely *Apus australiensis*.

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